BIOLOGY OF THE THYSANOPTERA. II

DR. A. FRANKLIN SHULL

UNIVERSITY OF MICHIGAN

II. SEX AND THE LIFE CYCLE

INTRODUCTION

From observations made on the abundance of males in several species, Jordan (1888) was led to believe that there might be among Thysanoptera, as in aphids, an alternating life cycle; that is, that there might be a series of parthenogenetic generations during the summer, followed by a generation of males and sexual females in the latter part of the summer or in the fall. Coupled with this he suspected that there were winged forms in the parthenogenetic part of the cycle, and at least occasional wingless individuals in the sexual phase.

Uzel (1895), however, was unable to detect any indications of such a cycle. He held that there could be no question of parthenogenesis in a species in which males were abundant all the time or at intervals. Only in species in which the males were too rare to impregnate all the females would he admit parthenogenesis. To prove, in such a species, an alternating cycle like that of the aphids, it must, in Uzel's opinion, be shown that the males are abundant only at certain seasons. As Uzel was acquainted with no European species in which males were plentiful at but one season, he rejected Jordan's suggestion regarding an alternating cycle, and his view seems to have been accepted by thysanopterists since that time.

To Uzel's argument it may be objected that the presence of males, and even the occurrence of copulation, is no proof that parthenogenesis is wanting. For among the aphids and rotifers, the parthenogenetic and sexual females exist side by side. Nor is parthenogenesis in these two groups facultative (optional), as Uzel appears to assume for Thysanoptera; a female is either only

sexual or only parthenogenetic. Moreover, in the rotifers, females incapable of fertilization copulate as frequently as do those requiring fertilization, as was first shown by the work of Maupas (1890) on the rotifer *Hydatina*.

Presence of males and occurrence of copulation are, therefore, no proof of sexual reproduction. But even if we accept, as Uzel does, this criterion of sexuality, Jordan's view that there may be an alternating cycle would receive some support if it could be shown that males are more abundant at one season of the year than at other times. Casual observations made by me several years ago seemed to indicate this seasonal variation in the abundance of males. As the data then available were meager, no conclusion was drawn, but I subsequently undertook to obtain such data on a larger scale, by making extensive collections at all seasons of the year to determine the sex ratio. The following pages give these data, along with other observations bearing on sex or the life cycle.

I desire to acknowledge the assistance of my wife, by whom much of the labor of determining species and counting the sexes was done.

The Sex Ratio in Various Species of Thysanoptera

In making collections for the purpose of determining the sex ratio, the food plants were examined very carefully, torn apart if necessary, and every individual captured. This precluded the possibility of obtaining an erroneous sex ratio because one sex was more easily disturbed than the other. A few individuals escaped, but they could not have affected the sex ratio very greatly, and it was known from their size that they were sometimes of the one sex, sometimes of the other.

The sex in the suborder Terebrantia is readily determined by the presence of an ovipositor in the female and the rounded end of the abdomen in the male. In the suborder Tubulifera, the sex in *Anthothrips verbasci* was determined by the presence of two short, heavy spines,

one on each side of the abdomen of the male, near the end. As the specimens, when placed on a microscope slide, nearly always lie either on the dorsal or ventral side, these spines are nearly always readily visible if present. I used this criterion (mentioned in the re-description of the species by Hinds, 1902) only after having taken eleven pairs of this species copulating in nature, and observing in every case that the male possessed these spines, and that in the female they were wanting. In other Tubulifera, *e. g.*, *Anthothrips niger,* sex was determined by the longitudinal chitinous rod in the next to the last abdominal segment of the female. When the specimens were too opaque to observe this rod, they were cleared by boiling in caustic potash.

The data from these collections are given in the accompanying table. Unfortunately the collections could not all be made in one year, nor in the same locality. Those made from July 1 to September 18, 1912, were made at the University of Michigan Biological Station, Douglas Lake, Michigan; all others were made at Ann Arbor, Michigan. It is not probable that the results are greatly modified by collecting in two regions within the state. In this table the larvæ of all species are combined, as I am unable to distinguish with certainty the larvæ of several of the species here mentioned.

The important facts contained in this table are, it seems to me, the following:

Euthrips tritici appeared in spring at first only in the female sex. Males were first collected nearly a month later, and not until about the time fairly large larvæ were found elsewhere. Once the males appear, though their number fluctuates in the individual collections, they furnish a fairly constant proportion of the whole number (about one third).

The males of *Anthothrips verbasci* appear in the earliest collection of this species, and in considerable numbers throughout the season. The total proportion of males is 23 per cent., and the only considerable increases over

this percentage in individual collections are in the three collections made in August, and on October 7. Considering the large majority of females taken September 12, the abundance of males October 7 may be due in some way to

TABLE I

SHOWING NUMBER OF MALES AND FEMALES OF THE COMMONER SPECIES OF THYSANOPTERA CAPTURED AT INTERVALS DURING THE ACTIVE SEASON

Date	*Euthrips tritici*		*Anthothrips verbaski*		*Anthothrips niger*		*Thrips tabaci*		*Anaphothrips striatus*		*Thrips physopus*		*Chirothrips manicatus*		Larvæ, all Species
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	
Apr. 30, 1911	9	0													
May 5	7	0													
10	2	0													
17	17	0													
22	22	1					2	0			2	3			
24	30	2	174	30	20	0	6	0							7
June 1	41	17			18	0									6
7	40	62	52	10	42	0					4	7			3
15	21	27	47	8	18	0					1	2			25
21	87	11			4	0	25	0	1	0	0	1			1
29	11	6			4	0					2	7	1	0	5
July 3, 1912	14	25			1	0									46
4	21	7			7	0	1	0							72
5	3	0	82	29	2	0							2	0	1
11	0	3					1	0	95	18			187	1	16
16	7	2	43	25	7	0	16	0							3
17	6	1			31	0	42	0							
19	12	29					2	0	35	6			5	0	3
26			58	15											2
27	3	0							45	13					4
29	2	0					4	0			10	9			12
30													1	51	
31									42	15					1
Aug. 5	154	151							28	10	1	0			39
8	8	1	30	20					2	0	10	1			
9	16	13									1	0			
12													2	103	2
13			26	18											1
18	60	16					2	0			1	0			
20			18	17					39	48			2	36	21
21	40	3					10	0							13
Sept. 2	60	7					27	2	60	33					10
2, 1911	35	15			8	0	19	0			2	2			2
12			88	1											18
16	18	3					15	0					1	0	4
18, 1912									183	21					4
Oct. 7, 1911	32	13	23	27			19	0							12
14	18	4					11	0					2	0	
25, 1912	56	19					12	0			15	4			2
Nov. 9	27	3					12	0			1	0			
Total........	879	441	641	200	162	0	226	0	530	174	50	36	203	191	

the dying of their food plants; but the greater proportion of males throughout August is probably significant. It should also be stated that I have collected adults of this species, of both sexes, from dead mullein spikes in late winter.

Anthothrips niger was found only in the female sex. There are no records of males of this species, so far as I am aware, in any published work.

Thrips tabaci was taken almost exclusively in the female sex, the two males found September 2 being the only ones I have ever collected.

In *Anaphothrips striatus* the total number of males is less than 25 per cent. On August 20 and September 2 the proportion of males is considerably greater than 25 per cent., especially on the former date, while at other times the proportion was nearly always less. The collection on August 20 can hardly have been erroneous by chance, for the figures given for that date are combined figures for two collections from different localities. In one of these collections there were 13 females and 14 males, in the other 26 females and 34 males. This strengthens the probability that the excess of males is significant.

Thrips physopus was collected in small numbers, but shows a fairly constant proportion of males.

Chirothrips manicatus presents curious phenomena. All the collections up to the end of July were made on timothy heads in a small patch a few feet square near the laboratory. On July 11 careful search revealed numerous females, but only one male. By July 19 almost all the thrips of this species were gone; only 5 specimens were obtained, and these were females. Less than two weeks later, however (July 30), on other timothy heads in the same small patch, there were found 51 males and but 1 female. No living thrips were taken here later, as the timothy died; but subsequent collections elsewhere, from timothy and bluegrass, show again almost exclusively males.

Additional Data Bearing on the Life Cycle and Sex

In view of the fact, to be discussed later, that *Anaphothrips striatus* has hitherto been known almost exclusively in the female sex, and is known to reproduce parthenogenetically, and the fact that in the collections here recorded the males constitute nearly 25 per cent. of the total, the question arises, are these males functional? If not functional in this species, are the males functional in other species? A number of observations and experiments I have made bear on these questions.

A single pair of *Anaphothrips striatus* was found copulating in nature, which Uzel would have considered proof that parthenogenesis did not occur. The testes of the males are plainly visible without dissection. Suspecting that they might not be fleshy organs at all, but chitinized structures, perhaps vestiges of testes, I boiled a number of specimens in caustic potash. The testes disappeared, from which I judge they are not merely chitinous bodies. I can say nothing of their cellular nature, owing to the loss of material killed and fixed for that purpose. Numerous sections of another species *Anthothrips verbasci*, however, reveal well-developed testes. Cell divisions (probably the spermatocyte divisions) and nearly mature spermatozoa in bundles were observed in these sections. Though the number of chromosomes could not be determined, it is an interesting fact that spindles in side view usually showed a lagging chromosome.

Finally, with further regard to the functioning of males, I have attempted to breed several species parthenogenetically. The results in the case of *Euthrips tritici* were so far encouraging that two larvæ appeared on the plant on which virgin females had been previously placed. But in these cases I could not be certain that the food plant was uninfected. Experiments with *Anaphothrips striatus* and *Anthothrips verbasci* gave negative results, but in each case failure to obtain young by parthenogenesis may have been due to the conditions.

Some observations on the place of pupation may also

be here recorded. The rarity with which the pupæ of most species are discovered in collecting suggested that they might not pupate on the food plant of the larvæ. Some species of thrips, for example, the pear thrips (*Euthrips pyri*), are known to pupate in the ground (Moulton, 1912). Since many of the species included in Table I may be found on white clover, which was abundant at Douglas Lake, the place of pupation of these species was tested in the following manner. A mass of the flowers of white clover was collected. The flowers were gently squeezed for some time to drive out all the adults. They were then placed in a vessel under cover. After two days, when the flowers were thoroughly dried, they were again gently crushed to make sure that all adults were driven out. At intervals from one to two weeks afterward, 15 adult thrips appeared on the inside of the glass cover. These were of three species, *Euthrips tritici*, *Thrips tabaci* and *Anthothrips niger*.

I have also frequently observed the pupæ of *Anthothrips verbasci* in mullein spikes, those of *Sericothrips cingulatus* on white clover, the pupa of *Trichothrips tridentatus* under the bark of the white oak, where the larvæ and adults live, and that of an undescribed species on willow galls along with larvæ of the same species. I judge from these observations that the majority of thrips pupate on the plants on which the larvæ live, and that their rarity in collections is due merely to concealment and sluggish habits.

Discussion of the Results in Relation to the Life Cycle

From the data in Table I and the observations given above it is evident that there is considerable diversity in different species with regard to the life cycle, and diversity within the same species at different times or in different regions. First, as regards the mode of passing the winter, it would seem that in *Euthrips tritici* only the females survive that season. The reason for so believing

is that males could not be found in the spring until the females had been active long enough to have produced one generation of offspring. Males occur late in autumn, but must perish before the end of winter. Likewise, neither eggs nor larvæ live over winter, or larvæ would appear earlier in spring. In *Thrips physopus,* on the other hand, males were found as early as the females; hence, in the absence of any collection earlier than May 22, and in ignorance of the time required for development, I should assume that both sexes survive the winter. Both sexes of *Anthothrips verbasci* have been seen on dead mulleins in winter.

In species, like *Euthrips tritici,* whose males do not survive the winter, if fertilization of the early spring females takes place at all, it must occur in the fall. I do not regard my breeding experiments as proof of parthenogenesis in this species, but it is by no means improbable that parthenogenesis occurs. More rigorous experiments are needed.

As regards the mode of reproduction during the rest of the year, there is nothing in the sex ratio, as given in Table I, to suggest an alternating cycle in *Euthrips tritici.* In other species, it would be possible to interpret certain facts to mean that an alternation of parthenogenesis and sexual reproduction occurs, or did once occur. There is a well-marked increase in the proportion of males in *Anaphothrips striatus,* for example, in August. This is a particularly interesting species. Hinds (1902) saw only the female of this species, though he mounted and examined over a thousand specimens, and he bred it parthenogenetically in the laboratory for months. What purported to be the male was described by Cary (1902), from Maine, but the specimens described were evidently those of another species. The first males ever recorded were described by Shull (1909), two specimens among probably two hundred females. It is remarkable, therefore, that in the vicinity of Douglas Lake there should be nearly 25 per cent. of males. Whether

the presence of numerous males is dependent on climatic conditions, or whether it is a racial difference, there is at present no way of deciding. The weather was unusually cold during the summer in which these records were made, and it is desirable that the effect of temperature be experimentally determined. The presence of males in goodly numbers throughout the summer, the occurrence of copulation in nature, and the failure of an attempt to breed the species parthenogenetically, leave, as the only reason for suspecting that it may have been parthenogenetic at Douglas Lake, the fact that it is parthenogenetic elsewhere. But if the species is parthenogenetic in one region and sexual in another, it is not difficult to believe that it may be both parthenogenetic and sexual in the same region. It is difficult to decide whether the well-marked increase in the proportion of males in August and early September should be regarded as evidence of such an alternation, or as due to a period of cold weather or other climatic factor, or as a hereditary remnant of the sexual phase of an alternating cycle once possessed by the species. Only experiment, and perhaps cytological study, can decide this question.

A similar but less marked increase in the number of males is seen in *Anthothrips verbasci,* also in August. In that month the proportion of males rose from about 20 per cent. to 40, or even nearly 50 per cent. In this species the increase may be due to the late date at which the first brood of larvæ becomes mature. The life history of this species is longer than that of most of the suborder Terebrantia, and may appear to be still longer because enemies destroy many of the larger larvæ. For these reasons, in the region of Douglas Lake, the first generation of larvæ may not become mature until nearly August. If this assumption is correct, the proportion of males found prior to August is the proportion that survive the winter. This explanation receives support from the cytology of the germ cells. As stated above, there is a lagging chromosome in the spermatocyte divisions, which suggests

the probability that there are two classes of sperm associated with sex, as in the bugs and many other animals, and that therefore the sexes should be approximately equal in numbers. The 40 to 50 per cent. of males in August accord fairly well with this explanation.

This explanation would not, however, account for the increase in the number of males in late summer in a species whose life history is much shorter than that of *Anthothrips verbasci*. Thus, in *Anaphothrips striatus*, Hinds states that the entire life history is passed through in 12 to 30 days. Even in a cold season, such as that of 1912 at Douglas Lake, therefore, the life history can not have been so long that the first adults would emerge in the middle of August. The increase in the number of males of *Anaphothrips* in August and September is not to be explained, therefore, as due to the first appearance of a new brood at that time.

Thrips tabaci likewise affords interesting, even if meager, evidence regarding the seasonal occurrence of males. In this species males are exceedingly rare. Hinds (1902) redescribed the male in quotation marks, from which it is to be inferred that he did not have specimens. In my own collecting, though the females were quite common, I never saw a male until the summer of 1912. Then two specimens were taken September 2, as shown in Table I. These irregularly occurring males can hardly be functional, so that *Thrips tabaci* is still probably to be regarded as wholly parthenogenetic. But their appearance in late summer may be the vestige of a former sexual phase, and may be caused now, as the sexual phase probably was in part formerly caused, by climatic conditions.

Chirothrips manicatus presented, at Douglas Lake, an anomalous condition. As shown in Table I, and stated more explicitly above, females were abundant in a given small area early in July, but practically no males were present. Then, so far as I could determine by painstaking collections, the females disappeared; almost no adults of either sex, and not many larvæ, were to be found. Two

weeks later, however, males were found in the same area in large numbers. As these males were wingless, they had probably not immigrated. The only other explanation that occurs to me is that the larvæ were present in considerable numbers at the time of the earlier collections, but in the flowers, not among the spikelets of the timothy, so that I did not discover them; and that the female larvæ reached maturity much earlier than the males. In any case, it is difficult to see how the males can have been functional, when the two sexes occurred at different times. If such conditions recur frequently, *Chirothrips manicatus*, even though it produces many males, must be parthenogenetic.

SUMMARY

The principal conclusions reached in the second part of this work may be stated as follows:

Some species of Thysanoptera pass through the winter in both sexes, in others the males perish. In none of those studied does the egg or larva live over winter.

Pupation of most of the species of Thysanoptera studied occurs on the food plants where the larvæ live, notwithstanding that the pupæ seldom appear in collections.

From the determination of the sex ratio, *Euthrips tritici* shows no indication of an alternating life cycle. It is probably sexual throughout the active season, though this is not proven.

Chirothrips manicatus occurred abundantly in both sexes, but the two sexes appeared at different seasons. The explanation of this phenomenon is doubtful.

An increase in the number of males in *Anthothrips verbasci* in late summer may be explained as due to the great length of the life history and to selective mortality during the winter, without assuming an alternating life cycle.

Anaphothrips striatus, a species which has hitherto been known almost wholly in the female sex, produced about 25 per cent. of males at Douglas Lake. This may

be due either to climatic conditions or to racial differences. Sexual reproduction was not wholly proven, but seems probable. An increase in the number of males in late summer in this species and in *Thrips tabaci* might be interpreted as indicating a sexual phase, or the vestiges of a sexual phase that existed in the species formerly. Jordan's belief in an alternating life cycle, which was rejected by Uzel, thus receives some measure of justification.

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